

BOWERBIRD (PTILONORHYNCHIDAE) BIOMETRICS, WITH OBSERVATIONS ON SEXUAL DIMORPHISM AND INTRASPECIFIC VARIATION

CLIFFORD B. FRITH AND DAWN W. FRITH

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Australasian bowerbirds (Ptilonorhynchidae) belong to 18 or 19 species made up of 35 subspecies. Comprehensive biometrical data are presented for the Ptilonorhynchidae. Mean values and ranges of measurements of each species and subspecies are given, and interspecific and intraspecific variation in size and body proportions discussed. These and plumage traits are used to assess species and subspecies. We accept 20 species including 31 subspecies. *Ailuroedus crassirostris*, *Sericulus ardens* and *Chlamydera guttata* are maintained as species, while *C. nuchalis* subspecies are reduced from four to two. *Ailuroedus melanotis joanae* and *Chlamydera guttata carteri* are considered valid and *Sericulus chrysocephalus rothschildi* invalid. □ *Bowerbird, biometrics, sexual dimorphism, variation.*

Clifford B. Frith and Dawn W. Frith, 'Prionodura', P.O. Box 581, Malanda 4885, Australia; 8 May 2000.

Gilliard (1969) considered the Australasian bowerbirds (Ptilonorhynchidae) consist of 8 endemic genera, containing 18 species, with 32 subspecies. With subsequent revisions the present consensus has 18 or 19 species, and 35 subspecies (Beehler & Finch, 1985; Christidis & Boles, 1994; Frith et al., 1995; Frith & Frith, 1997a,b, 1999; Schodde & Mason, 1999).

Bowerbirds attract attention particularly because of the elaborate bowers ♂♂ build and decorate. These are related to their polygynous mating system and associated ♂ promiscuity (Gilliard, 1963; Borgia, 1986). Adult ♂♂ show remarkable interspecific diversity of ornate plumages, bower structures and decorations, courtship, and vocalizations. They use these in complex and ritualised displays at traditional sites (Diamond, 1986; Borgia, 1986, 1995; Frith, 1970; Frith & Frith, 1989, 1990, 1993, 1994, 1995a, 2000a,b,c,d; Johnsgard, 1994). Size differences between the sexes (♂♂ typically larger than ♀♀) are particularly pertinent in most polygynous vertebrates but no comprehensive review of size variation among bowerbirds has been published.

Gilliard (1969) provided size ranges for basic traits without indicating either sample sizes or subspecific groupings. Cooper & Forshaw (1977) gave measurements for "five or more specimens" of species. Measurements for some subspecies appear in Schodde & Mason (1999), without sample sizes or means. Biometrical data are available for *Amblyornis* (Schodde & McKean, 1973; Frith & Frith, 1997b, 1998),

Sericulus (Diamond, 1969; Lenz, 1999), *Ptilonorhynchus* (Schodde & Mason, 1999) and *Chlamydera* (Frith & Frith, 1997a, 1999).

Some bowerbird subspecies have been distinguished on geographical plumage and size variation (Gilliard, 1969; Schodde & McKean, 1973; Diamond, 1969, 1972; Coates, 1990; Lenz, 1999; Frith & Frith, 1997a,b; Schodde & Mason, 1999). We examine our biometrical data with respect to subspecies defined by these authors. Differences in average population sizes has limitations, given that size is a continuously varying trait. While this is not a formal taxonomic revision, we record key broad plumage characters where appropriate.

Genera and their sequence herein are a combination of those of Beehler & Finch (1985) and Christidis & Boles (1994). We largely follow Gilliard (1969) at the species and subspecies levels. That is, as taxa are acknowledged in Gilliard's species accounts. Since Gilliard's (1969) text was written *Ailuroedus buccoides oorti* (Mees, 1964), *Se. chrysocephalus rothschildi* (Schodde & Mason, 1999), *C. nuchalis oweni* and *C. n. yorki* (Frith & Frith, 1999) have been rejected. *Al. b. cinnamomeus* (Mees, 1964), *Al. melanotis joanae* (Ford, 1977), *Am. macgregoriae kombok*, *Am. m. nubicola* (Schodde & McKean, 1973), *Am. m. amati* (Pratt, 1982), *Am. m. lecrovae* (Frith & Frith, 1997b) and *C. guttata carteri* (Frith & Frith, 1997a) have been erected or resurrected. *C. m. guttata* and *Se. aureus ardens* have been raised to species level (Schodde, 1982; Lenz, 1999). We agree with

TABLE 1. Measurements (mm) and weights (g) for *Ailuroedus buccoides*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
<i>A. b. buccoides</i>								
Males: adult								
Mean	138	90	38.3	63.1	31.4	10.1		172
SD	7.77	5.65	2.31	0.99	2.05	0.71		
Min	123	83	34.1	62.4	27.6	8.5		
Max	143	99	41.6	63.8	33.3	11.1		
n	16	14	14	2	12	13		1
Females: adult								
Mean	130	85	36.9	58.2	29.5	9.5		151
SD	7.14	5.26	1.97	2.24	1.53	0.66		141
Min	118	78	34.8	55.0	27.4	8.3		150
Max	140	94	41.0	61.1	32.2	10.7		152
n	15	15	14	7	15	15		2
<i>A. b. sibirii</i>								
Males: adult								
Mean	130	92	38.8	59.7	30.5	9.6		142
SD	3.44	3.13	1.18	1.84	1.46	0.49		5.32
Min	130	85	36.3	57.8	28.0	8.9		135
Max	143	96	40.7	62.6	33.4	10.9		150
n	16	16	16	11	16	16		7
Females: adult								
Mean	132	86	37.2	57.6	28.6	9.1		140
SD	1.91	2.61	1.12	2.14	1.32	0.33		9.05
Min	129	82	35.4	55.8	26.9	8.4		126
Max	136	90	39.1	62.2	31.7	9.5		150
n	12	12	12	7	11	12		7
<i>A. b. geisterorum</i>								
Males: adult								
Mean	134	90	37.7	58.4	30.4	9.7	12.6	139
SD	4.18	3.44	1.57	1.36	1.06	0.60	0.78	12.26
Min	125	84	32.9	56.3	27.6	8.5	12.0	110
Max	143	98	40.6	62.3	32.5	10.7	13.1	159
n	42	39	42	36	42	41	2	23
Females: adult								
Mean	129	85	36.1	57.0	29.1	9.1	11.7	128
SD	4.57	3.30	1.31	1.59	0.91	0.51	0.55	11.82
Min	118	79	33.3	53.9	26.5	8.1	11.1	100
Max	139	93	38.2	60.7	30.9	10.3	12.3	150
n	46	45	45	30	44	44	5	30
<i>A. b. annamensis</i>								
Males: adult								
Mean	137	91	39.1	59.1	30.6	10.0		150
SD	4.48	2.79	1.46	1.83	1.33	0.51		
Min	130	85	37.0	56.4	27.1	9.2		
Max	147	95	41.7	62.4	32.6	11.2		
n	19	18	19	11	18	18		
Females: adult								
Mean	133	87	37.0	57.0	29.2	9.6		130
SD	3.67	2.24	1.19	0.79	1.41	0.52		
Min	129	84	35.4	56.1	27.1	8.7		
Max	141	92	38.3	58.3	31.6	10.5		
n	17	17	16	9	17	16		1
All subspecies								
Males: adult								
Mean	136	91	38.3	59.6	30.6	9.8	12.6	141
SD	5.10	3.75	1.71	1.62	1.29	0.69	0.78	12.27
Min	123	85	32.9	56.3	27.1	8.5	12.0	110
Max	149	99	41.7	63.8	33.9	11.2	13.1	172
n	93	87	91	60	91	68	2	32
Females: adult								
Mean	131	86	36.5	57.3	29.1	9.2	11.7	129
SD	4.91	2.78	1.45	1.68	1.20	0.55	0.55	13.05
Min	118	78	33.3	53.9	26.5	8.1	11.1	100
Max	141	96	41.0	62.2	32.2	10.7	12.3	152
n	90	89	87	52	67	67	5	40

these decisions. *Al. crassirostris* was considered a subspecies of *Al. melanotis* by Schodde & Mason (1999) but see our discussion herein. We

use vernacular names of Beehler & Finch (1985) and Christidis & Boles (1994) except Spotted Catbird for *Al. melanotis* and Yellow-breasted Bowerbird for *C. lauterbachii*; we retain the traditional Black-eared Catbird and Lauterbach's Bowerbird, respectively.

METHODS

We examined all sexed skin specimens with a locality of origin in 32 collections (see Acknowledgements). The catalogue numbers of all specimens used and the measurements taken to produce Tables 1-21 are tabulated and lodged in the library of the Queensland Museum; copies may be obtained from the authors or from the library. Standardized measurements were taken by CBF with the same instruments. 'Wing length' is the flattened and straightened chord, measured with a stopped steel decimal rule. 'Tail centrals' is the maximum length of the longest of the central pair of rectrices, from point of feather entry into skin to its terminal tip, and 'tail length' likewise but to the tip of the longest feather other than the central pair. Tails were measured with an unstopped narrow steel decimal rule. When central and outer tail rectrices were the same length, or <3mm different, only the longer (usually 'tail length') is given. Where there is intraspecific variation, both are given. Other measurements were taken with new line-pointed steel electronic digital vernier callipers (checked/zeroed daily) to the nearest whole decimal point. 'Bill length' is from the union of bill and fore skull (cranio-maxillary hinge) to the upper mandible tip. We measured bill lengths only from specimens with a complete upper mandible and on which the undamaged cranio-maxillary hinge could be confidently located. 'Bill width' and 'bill depth' (of fully closed bills only) were taken at the anterior nostril edge. 'Total head length' is the maximum distance from rear skull to the upper mandible tip, measured only from specimens retaining sufficient skull bone. Some specimens may appear complete in this respect but are not so total head length figures are minimums. 'Tarsus length' is from the intertarsal joint to the lower edge of the last undivided scute (scale) before the toes diverge. Our measurements of live wild birds were generally similar to those from museum specimens, but we only include live bird measurements where samples of museum specimens are relatively small. Measurements of live birds included are for 10 immature/subadult ♂ *Sc. dentiostri*; 4 adult and 2 immature ♂ and

2 ♀ *Archboldia papuensis sandfordi*; 7 subadult and 42 immature ♂ *Prionodura newtoniana*; 3 adult, 1 subadult and 17 immature ♂ *Pt. violaceus minor*.

As a large majority of Schodde & Mason (1999) wing and tail length ranges fall well within the limits of our ranges we conclude that their samples were smaller. From our samples we evaluate previous assessments of several size-related characters. Gilliard (who used both "culmen" and "culmen from base"), Cooper & Forshaw (1977) and Schodde & Mason (1999) present "culmen length" or "exposed culmen", as opposed to bill length. Culmen length is the same as exposed culmen, and is measured from where anterior forehead feathers no longer cover the culmen to the bill tip, and is not of an entire structure. Thus culmen measurements are shorter, often exclusively, than our bill lengths. Culmen length appears more subjective and variable than bill length and may mislead as it is not structural bill length (Frith & Frith, 1997c: 173; Frith & Beehler, 1998; *Pt. violaceus* below).

Some ♂♂ have a nuchal or fuller crest, which was measured from the posterior crest base to its tip (Schodde & McKean, 1973). We also measured crest length as viewed from above (Frith & Frith, 1997b, 1998). All measurements are in mm. Weights (in grams) were noted from specimen labels. We include additional weights obtained from live birds as follows: 27 adult ♂ and 36 ♀ *Al. m. maculosus*; 46 adult and 10 immature ♂ and 1 ♀ *Sc. dentirostris*; 3 adult and 2 immature ♂ and 2 ♀ *Ar. p. sandfordi*; 79 adult, 7 subadult, 42 immature ♂ and 12 adult ♀ *Pt. newtoniana*; 3 adult, 1 subadult, and 32 immature ♂ *Pt. v. minor*; 14 adult, 4 subadult ♂♂, and 1 adult ♀ *C. maculata*; 5 adult ♂ *C. nuchalis*. Differences in weight between sexes are commented upon only where samples are adequate, because body weight is subject to bias with respect to time of day/year recorded.

Data are reported for adult samples unless otherwise stated. Data for markedly sexually dimorphic species in which ♂♂ may have an adult, subadult (i.e. trace to almost complete adult ♂ plumage intruding into ♀-type), and immature (purely ♀-type) plumage are presented separately for each age group. For monomorphic species, in which adult ♂♂ and ♀♀ are similar but ♂♂ have a discernibly different immature plumage, data are given separately. Data for ♀♀ are of adults, but some samples might inadvertently include the odd younger

individual, given the similarities of ♀ plumages. We exclude conspicuously smaller individuals (i.e. presumed juveniles-immatures). We do not describe plumages of monotypic species or those of nominate subspecies as these are widely available (Rand & Gilliard, 1967; Gilliard, 1969; Cooper & Forshaw, 1977; Beehler et al., 1986; Coates, 1990; Donaghey, 1996; Schodde & Mason, 1999). In a few instances we refer to numbered colours of Smithe (1975), with his nomenclature indicated by capitalisation. Geographical ranges indicated do not include controversial or vagrant records. West Papua (WP) was Irian Jaya.

SYSTEMATIC NOTES

Family PTILONORHYNCHIDAE

Ailuroedus buccoides (Temminck in Temminck & Laugier, 1835) White-eared Catbird (Tables 1 and 22)

♀♀ average 5% smaller than ♂♂ in tail, tarsus and bill lengths, 6% in bill width, 7% in bill depth and 9% in weight. Tail/wing ratio is 66%, tarsus/wing 28% and bill/wing 22%. Measurements and body size ratios are near uniform across subspecies, except in *geislerorum* which has fractionally shorter wings. We follow Mees (1964) in synonymising *oorti* with *A. b. buccoides*.

Ailuroedus buccoides buccoides (Temminck in Temminck & Laugier, 1835)

Al. b. oorti Rothschild & Hartert, 1913.

♀♀ average 6% smaller in wing, tarsus and bill lengths and bill width than ♂♂. Sexual size dimorphism is little different in the other subspecies. Characterised as "Under surface pale cinnamon with large black dots; crown brown, usually tinged with greenish." (Mees, 1964: 127). Range: W Papuan Islands (Is) and Vogelkop lowlands, coastal W and central Geelvink Bay to Siritwo River (R) in north New Guinea. Triton Bay E to upper Fly R in south New Guinea (NG).

Ailuroedus buccoides stonii Sharpe, 1876

Underparts deep cinnamon, black spots smaller than other subspecies. Crown dark blackish-brown, sometimes tinged greenish, distinctly blacker than in other subspecies. Range: SE coastal Papua New Guinea (PNG) from Amazon Bay to upper Purari R, including

TABLE 2. Measurements (mm) and weights (g) for *Ailuroedus crassirostris*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
Males: adult							
Mean	166	124	47.1	64.7	34.0	10.0	215
SD	7.35	5.60	1.95	2.50	1.68	0.56	35.41
Min	151	111	40.4	59.6	31.2	8.4	167
Max	179	139	50.0	69.6	38.0	10.8	289
n	38	36	37	25	37	36	13
Females: adult							
Mean	161	120	45.8	63.1	33.2	9.8	193
SD	6.03	5.35	2.16	2.15	1.64	0.51	15.20
Min	150	108	41.6	60.4	30.5	8.9	169
Max	172	127	49.3	67.3	36.9	10.8	211
n	25	25	26	11	26	26	7

the Karimui, Bomai, Soliabeda areas, E Highlands (Diamond, 1972).

Ailuroedus buccoides geislerorum
Meyer, 1892

Al. b. molestus Rothschild & Hartert, 1929.

Underparts as in nominate form but, unlike it and all other subspecies, crown light tan brown. The pure white ear covert feathering extends forward onto the lower lores. Range: Japen Is and north NG from Mamberamo R to Collingwood Bay, PNG.

Ailuroedus buccoides cinnamomeus
Mees, 1964

Underparts save throat deep cinnamon, as in *stonii*, with large black spots. Crown as nominate *buccoides* but on average tinged more green. We found, as did Mees (1964), that at the eastern end of its range 5 of 6 individuals had a darker crown colour, thus approaching *stonii* further east. Range: south WP from Mimika R, E to upper Fly R and Lake Kutubu, PNG.

Al. b. geislerorum is distinctive in its paler tan crown and white ear covert feathering extending forward to include the lower lores. *Stonii* is equally distinctive in its black crown and lores, contrasting pure white ear coverts, and deep cinnamon ventral colouration. *A. b. buccoides* and *cinnamomeus*, have brown crowns (variably washed greenish). Both have heavy black spotting on the white ear coverts, but *cinnamomeus* has considerably darker cinnamon underparts and usually more white (as opposed to dark brown in *buccoides*) lower lores. These differences are greater than the "northern form, brown cap" and "western and southern form, blackish cap" defined for field use (Beehler et al.,

1986), which may give the erroneous impression of only two subspecies.

***Ailuroedus crassirostris* (Paykull, 1815)**
Green Catbird
(Tables 2 and 22)

♀♀ average 10% lighter than ♂♂. Adult tail/wing length ratio 74%, tarsus/wing length 28% and bill/wing length 20%. Thus this species is proportionately longer-tailed than *Al. m. maculosus* (Table 3), to its N within Australia Mean bill/tarsus length is 72.3% compared to 77.5% in *Al. m. maculosus*. Range: Coastal Australia from Dawes Range (Ra), Qld to E of Canberra in NSW.

Ailuroedus crassirostris has been considered the southern subspecies of *Al. melanotis* (Pizzey, 1980, 1997; Simpson, 1984, 1999; Schodde, 1976 a,b, 1986) or a separate species (Mack, 1953; Slater, 1974; Slater et al., 1989). Schodde & Mason (1999) argue that "*maculosus* cannot be combined with *melanotis* without bringing in *crassirostris* as well", an argument we do not accept. While the 10 subspecies of *Al. melanotis* demonstrate considerable geographical variation, they all share the traits of a dark crown spotted with conspicuous white to buff markings, strongly contrasting black chin feathering and ear coverts that give a "black-eared" appearance, and broad dusky edging to predominantly whitish throat and chest feathering to give a scalloped appearance. As *Al. crassirostris* (a) lacks the first three characters, (b) has a green throat and chest finely streaked by white central feather lines, (c) is longer tailed and shorter billed than *Al. m. maculosus* and (d) is geographically isolated by more than 600 km, we treat it as a distinct species.

We find the acceptance of *Al. crassirostris* as a species, on morphological and zoogeographical grounds, consistent with similar treatment of *C. guttata* as distinct from *C. maculata* (Christidis & Boles, 1994:74; Schodde & Mason, 1999). The latter are separated by 250 km. *Al. crassirostris* evolved in isolation from *Al. melanotis* stock, the issue being to what level of taxonomic significance it has differentiated. Equivocal (Schodde & Mason, 1999) allele frequency data (Christidis & Schodde, 1992) supported separation of *crassirostris* as a species. Given the foregoing, and that tissue samples remain unavailable for the Aru Is population of *Al. m. melanotis*, for *Al. m. arfakianus*, and for other montane populations (Schodde & Mason, 1999), we concur with Christidis & Boles (1994) in

maintaining *Al. crassirostris* as a separate species.

***Ailuroedus melanotis* G.R. Gray, 1858**
Black-eared Catbird
(Tables 3 and 22)

Body ratios are similar to those of *Al. crassirostris*. ♀♀ average 5% smaller than ♂♂ in bill width and 8% in weight. Proportions of size sexual dimorphism among the various characters vary slightly between subspecies, but no pattern is evident. Subspecies are generally similar in leg/wing and bill to wing length ratios, but there is some variation in tail/wing length.

Ailuroedus melanotis melanotis
(Gray, 1858).

Darker areas of head plumage and dark edging to the upper breast feathers are blackish to black. Range: Aru Is and Trans-Fly lowlands of south NG.

Ailuroedus melanotis arfakianus
Meyer, 1874

Tail/wing length ratio is 68%. The tail is thus proportionately short, as is that of *joanae* (at 69%). Throat much darker than in *melanotis melanotis*, being black spotted with dirty white to pale buff down to the chest. The latter is not marked blackish as in *melanotis melanotis*, but is darker green marked with narrow and pointed pale buff feather centres. Pale patch behind black ear coverts large and clear white; large spotting on the black crown paler (white or almost so) than in *melanotis melanotis*. Range: Arfak and Tamrau Mountains (Mts), Vogelkop, possibly also Kumawa Mts, WP (Diamond, 1985).

Ailuroedus melanotis maculosus
Ramsay, 1874

Head, nape and upper back less black and far paler than in nominate form, with dark brownish feather edges. Upper back spotting very small, pale buff and feathers lacking blackish edging. Green of back and upper tail paler and slightly more yellowish than in nominate form. Underparts far paler buffy-white, more green, than in *melanotis melanotis* and feathers with broad brown-green edges. Chest far paler and less heavily marked than *melanotis melanotis*. Galbraith (in Mees, 1982) found 4 ♂♂ and 2 ♀♀ had mutually exclusive maxilla depths (11-12.5 versus 10-10.5, respectively) which Mees (1982) thought separated the sexes. In measuring bill depth of 5 of each sex, we found considerable

TABLE 4. Measurements (mm) and weights (g) for *Scenopoeetes dentirotis*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
Males: adult								
Mean	149	104	31.7	57.6	30.7	10.3	13.5	158
SD	3.86	2.26	1.09	1.77	1.15	0.47	0.43	11.12
Min	141	100	29.4	52.1	28.3	9.4	12.6	132
Max	156	108	34.0	59.8	32.9	11.2	14.4	199
n	35	35	34	23	35	35	20	51
immature/subadult								
Mean	150	103	31.5	58.7	30.0	10.4	14	164
SD	2.81	1.55	1.81	1.00	1.50	0.31	0.51	12.48
Min	146	101	28.0	57.4	27.2	10.0	13.3	151
Max	155	106	33.0	59.7	31.4	10.7	14.9	185
n	10	8	7	5	7	7	7	10
Females: adult								
Mean	146	101	31.6	58.1	31.0	10.7	13.6	169
SD	3.16	3.08	1.42	1.37	1.16	0.39	0.61	12.62
Min	138	96	29.4	54.0	28.1	9.9	12.7	157
Max	152	107	34.5	59.7	33.0	11.3	14.6	182
n	25	25	25	16	24	26	8	3

overlap. Range: Australian Wet Tropics, from Mt Amos to Seaview-Paluma Ra, Queensland (Qld).

Ailuroedus melanotis melanocephalus
Ramsay, 1883

Tail/wing length ratio is 78%. Like nominate form but underparts generally darker, blacker on chest and throat, and more rufous below. Crown blacker, as the buff spots are slightly smaller and/or sparser (more so in two birds from 'Yule I.'). Range: mountains of SE NG, west to Herzog Mts in north and Mt Karimui in south, including Owen Stanley, Hydrographer, Astrolabe, Wharton and possibly Kratke Mts.

Ailuroedus melanotis jobiensis
Rothschild, 1895

Dorsally like *melanotis melanotis* but spotting on the blackish crown less pure white, more buff. Ventrally quite different in that the chin, throat and upper chest are blackish with only fine buff spotting thereon. Remaining underparts similar to, but darker than *melanotis melanotis*. This subspecies is more like *guttaticollis* ventrally, the throat to upper chest being darker due to smaller pale spotting. White patch behind black ear coverts more obvious than in most subspecies. Range: Bewani, Torrielli, Prince Alexander Mts, middle Idenburg R, and (tentatively) Adelbert Mts, NG.

Ailuroedus melanotis guttaticollis
Stresemann, 1922

Like nominate form but spotting of crown to upper back more rufous, less buffy. Throat and

chin much darker and underparts generally more rufous. In colour and markings indistinct from *jobiensis*. Range: Sepik and (tentatively) Jimi R, PNG.

Ailuroedus melanotis astigmaticus

Mayr, 1931

Tail/wing length ratio is 81%, this being the longest-tailed subspecies. Like *melanotis melanotis* but crown blacker, with fewer, finer, and paler spots. Range: mountains of Iluon Peninsula, PNG.

Ailuroedus melanotis facialis Mayr, 1936

Tail/wing length ratio is 71%. Like nominate form but throat darker, less white and more buff. Spotting of crown and upper back much darker, more cinnamon (123A to 123). This is not a "poorly differentiated subspecies" (Cooper & Forshaw, 1977) when compared with its nearest conspecific population of *Al. m. jobiensis*, as the latter has a much darker throat, breast, and crown. Range: Nassau and Oranje Mts, WP.

Ailuroedus melanotis misoliensis

Mayr & de Schaunsee, 1939

Like *arfakianus* but blacker at base of throat, and averaging much larger but with some overlap (Mees, 1965). Range: Misool I, WP.

Ailuroedus melanotis joanae

Mathews, 1941

Tail/wing length is 69%, the tail being similar in length to the other Australian subspecies *maculosus* (68%). Compared to *maculosus*: smaller, blacker on crown, nape, and mantle, less black on face and chin, throat whiter, lower breast, flanks, belly, ventrals and under tail coverts far cleaner (less marked with buff-green feather edging) and thus clean yellowish on these underparts. Differs from other Australian catbirds in having all underwing coverts pure white (save a few exceptions involving only the outermost greater primary coverts). In *Al. crassirostris* and *Al. u. maculosus* these feathers are centrally heavily pigmented with blackish-grey and their edges dirty whitish with the faintest of greenish wash in places. Scalloping on chest notably blacker than on the other Australian subspecies, but less black than on the nominate form in New Guinea to which *joanae* is overall more similar than it is to *maculosus*. Range: QLD, Australia. Pascoe R and Iron Ra areas to Rocky R, Mellvraith Ra, Cape York Peninsula.

Ford (1977) resurrected *joanae* and defined some plumage characters (enlarged upon by Schodde & Mason, 1999) distinctive from *maculosus*. Ironically, the only character Mathews (1941) used in naming *joanae*, that it is smaller than *maculosus*, is invalid. To test this we compared sizes of *joanae* (2 ♂♂ and 5 ♀♀, given that we agree with Ford (1977) that the holotype is ♀) with northernmost *maculosus*, from Mt Finnegan (4 ♂♂), Gap Creek, 7 km N of Bloomfield (3 ♂♂, 1 ♀), Granite Creek, Bloomfield R (3 ♂♂, 4 ♀♀), and Big Tableland (2 ♂♂, 1 ♀). Results show *joanae* no smaller than closest *maculosus*.

Scenopoeetes dentirostris (Ramsay, 1876)

Tooth-billed Bowerbird

(Tables 4 and 22)

♀♀ 7% heavier than ♂♂, but this may be due to time of year few weights were taken. This species has by far the shortest proportional tarsus length and is arboreal except when, rarely and briefly, on their forest floor courts (Frith & Frith, 1994). Immature/subadult ♂♂, of Table 4, were all live court-attending birds identifiable as such by their pale mouth (black in adult ♂♂; Frith & Frith, 1995a). Measurements of wing length by Cooper & Forshaw (1977) are near the higher limit of our sample, while most of their other measurements are outside our ranges. As this is the only potentially lekking bowerbird (Frith & Frith, 1995a) in which males form an exploded (voeal rather than visual contact (Johnsgard, 1994)) lek it is surprising to find adult ♂♂ little larger than ♀♀ (and less so than in monogamous *Ailuroedus*). While *Scenopoeetes* has long been considered closest to monogamous *Ailuroedus*, on similarities in plumage and egg colour, behavioural and molecular data indicate its closer relationship to typical, polygynous, genera particularly *Amblyornis* (Frith & Frith, 1993; Kusmierski et al., 1993, 1997; Schodde & Mason, 1999). Range: Australian Wet Tropics uplands, from Mt Amos to Mt Elliot, Qld.

Archboldia papuensis Rand, 1940

Archbold's Bowerbird

(Tables 5 and 22)

♀♀ 8%, 22% and 9% shorter in wing, tail and tarsus lengths, respectively, than ♂♂ but the same in bill length. With a tail/wing length ratio of 96% (103% for ♂♂ only) this is the longest-tailed bowerbird. We assume Gilliard (1969) and Cooper & Forshaw (1977) included some younger individuals in their adult ♂♂

TABLE 5. Measurements (mm) and weights (g) of *Archboldia papuensis*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
<i>A. p. papuensis</i>									
Males: subadult									
Mean	159	152	137	39.6	65.2	33.0	8.4		173
SD	2.1	5.7	5.7	0.9	1.5	0.2	0.3		3.5
Min	157	148	133	38.9	64.1	32.8	8.2		170
Max	160	156	141	40.2	66.2	33.1	8.6		175
n	2	2	2	2	2	2	2		2
immature									
Mean	158	135	125	42.2	64.0	32.8	8.2		
SD	3.50	9.68	7.27	1.28	1.01	1.45	0.36		
Min	156	127	120	40.8	62.9	30.7	7.7		
Max	163	148	136	43.9	84.9	34.1	8.5		
n	4	4	4	4	3	4	4		
Females: adult									
Mean	148	126	116	38.1	64.0	33.4	8.9		
SD	4.39	3.65	6.35	1.73	1.42	1.60	0.33		
Min	144	122	112	36.6	62.6	31.0	8.5		
Max	155	130	123	40.7	66.1	35.3	9.2		
n	5	5	3	5	5	5	5		
<i>A. p. sanfordi</i>									
Males: adult									
Mean	168	173	146	43.4	66.3	33.5	8.5	10	184
SD	3.39	8.59	7.29	1.70	1.30	0.91	0.56	0.43	3.88
Min	161	155	133	39.4	64.6	31.8	7.5	8.7	180
Max	174	189	165	45.9	69.8	35.9	9.4	10.3	190
n	21	20	18	21	15	20	20	9	6
immature									
Mean	165	152	137	43.4	66.3	33.6	8.3	9.9	186
SD	1.69	6.72	6.50	1.34	1.03	1.26	0.39	0.38	9.63
Min	163	145	132	41.7	64.4	31.5	7.8	9.6	170
Max	167	162	150	45.4	67.7	35.7	8.8	10.3	195
n	8	7	7	8	7	8	8	3	5
Females: adult									
Mean	158	140	130	40.4	65.3	33.5	8.7	10.0	176
SD	4.74	4.80	4.33	1.65	1.02	1.31	0.70	0.18	9.42
Min	148	132	125	37.1	64.0	31.5	7.8	9.8	163
Max	163	149	139	42.7	66.5	35.6	9.7	10.2	185
n	9	9	8	9	6	9	9	4	4
All subspecies									
Males: adult									
Mean	168	175	148	43.3	66.6	33.6	8.4	9.6	184
SD	3.45	8.25	6.62	1.57	1.32	0.93	0.58	0.18	3.88
Min	161	155	135	39.4	65.0	31.8	7.5	9.4	180
Max	174	189	165	45.5	69.8	35.9	9.4	9.8	190
n	17	16	14	17	11	16	16	5	6
subadult									
Mean	159	152	137	39.6	65.2	33.0	8.4		173
SD	2.1	5.7	5.7	0.9	1.5	0.2	0.3		3.5
Min	157	148	133	38.9	64.1	32.8	8.2		170
Max	160	156	141	40.2	66.2	33.1	8.6		175
n	2	2	2	2	2	2	2		2
immature									
Mean	163	146	133	43.0	65.6	33.4	8.3	9.9	186
SD	4.23	11.59	8.89	1.39	1.48	1.33	0.38	0.38	9.63
Min	156	127	120	40.8	62.9	30.7	7.7	9.6	170
Max	167	162	150	45.4	67.7	35.7	8.8	10.3	195
n	12	11	11	12	10	12	12	3	5
Females: adult									
Mean	154	135	126	39.5	64.7	33.5	8.8	10.0	176
SD	6.70	8.37	8.10	1.97	1.32	1.36	0.58	0.18	9.42
Min	144	122	112	36.6	62.6	31.0	7.8	9.8	163
Max	163	149	139	42.7	66.5	35.6	9.7	10.2	185
n	14	14	11	14	11	14	14	4	4

because their wing length ranges of 155-170 and 155-162 are small versus our 161-174. The two geographically isolated forms of this bird are considered separate species by some (Gilliard, 1951, 1958, 1959; Peckover & Filewood, 1976; Collar, 1986) and indistinct, or invalid, subspecies by others (Frith et al., 1995). While lack of adult ♂ specimens of *papuensis*

TABLE 6. Measurements (mm) and weights (g) of *Amblyornis inornatus*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
Males: adult								
Mean	134	95	93	36.4	60.7	30.1	8.4	128
SD	3.37	3.77	3.84	1.37	1.70	1.43	0.51	15.51
Min	129	88	84	34.0	57.2	27.4	7.3	105
Max	140	104	100	39.2	63.8	33.1	9.7	155
n	28	28	26	28	19	27	27	12
Females: adult								
Mean	130	91	91	35.2	60.2	30.2	8.6	121
SD	3.11	2.77	3.00	1.18	1.89	1.37	0.87	15.21
Min	125	85	84	33.4	57.8	27.9	6.9	105
Max	136	96	95	37.8	63.7	32.1	10.0	146
n	18	18	17	18	14	18	18	9

papuensis hampers comparisons, adult ♀♀ (Table 5) are smaller than those of *sanfordi*.

Archboldia papuensis papuensis Rand, 1940

The smaller subspecies, averaging 6% smaller in wing and tarsus length, and 10% in tail length (♀♀ only), but similar in bill size. This difference in tail length is exclusive, the range in this form being 122-130 but in *sanfordi* 132-149. The adult tail/wing length ratio averages 96% in ♂♂ and 85% in ♀♀. Plumage is generally less black, more grey, than that of *sanfordi*. Range: Ibele R (Balim Valley) to Lake Habbema region, Oranje Mts, Nassau Ra and Wissel Lakes, Weyland Mts area, WP.

Archboldia papuensis sanfordi Mayr & Gilliard, 1950

Larger than *papuensis papuensis* and plumages blacker. Tail/wing length ratio averages 103% in ♂♂ and 89% in ♀♀. Adult ♂♂ fully crested. Mean exposed crest length of 20 ♂♂ is 91 (77-98, SD 5.41). Range: Mt Hagen, Giluwe, Tari Gap and S Karius Ra (unconfirmed on Kubor Ra), PNG (Coates, 1990).

Amblyornis inornatus (von Rosenberg in Schlegel, 1873) Vogelkop Bowerbird (Tables 6 and 22)

♀♀ average fractionally smaller than ♂♂ in body sizes and weight. Both sexes in this and other *Amblyornis* are identical or similar in tail/wing length ratios (Table 21), a trait shared by *Scenopoeetes* among polygynous genera (and also by monogamous *Ailuroedus*). Range: Arfak, Tamrau, Wandammen, Kumawa, and Fakfak Mts, WP (Diamond, 1987; Uy & Borgia, 2000).

TABLE 7. Measurements (mm) and weights (g) of *Amblyornis macgregoriae*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
<i>A. m. macgregoriae</i>									
Males: adult									
Mean	135	87	85	37.4	57.9	28.0	7.6		120
SD	3.22	3.35	3.19	1.04	0.95	0.83	0.66		13.47
Min	129	81	79	35.5	55.4	26.8	6.7		104
Max	142	92	91	40.0	59.3	30.1	8.9		142
n	22	22	20	22	13	22	22		7
immature									
Mean	133	87	86	37.3	57.3	27.5	7.4		120
SD	3.84	3.55	3.49	1.43	1.16	1.23	0.48		8.22
Min	126	80	80	34.6	55.6	25.2	6.5		110
Max	139	92	91	40.6	60.1	29.9	8.2		199
n	22	21	19	22	16	22	22		14
Females: adult									
Mean	131	85	83.4	36.1	58.2	28.5	8.0	8.8	123
SD	3.42	3.12	3.02	1.10	1.54	0.82	0.50		5.71
Min	123	78	77	33.3	54.1	27.0	6.8		115
Max	138	90	90	38.0	59.9	29.6	9.3		130
n	26	26	22	28	19	26	25		7
<i>A. m. germanus</i>									
Males: adult									
Mean	130	87	84	36.3	57.8	27.1	7.3	8.6	112
SD	3.11	1.82	2.19	0.98	1.46	0.86	0.38		8.68
Min	124	85	81	34.9	56.0	26.0	6.6		104
Max	135	90	86	37.8	59.7	28.5	7.9		127
n	11	11	9	11	6	11	11		1
immature									
Mean	128	88	84	36.8	55.8	26.7	7.7		114
SD	2.56	2.26	3.33	0.88	1.38	1.18	0.31		2.87
Min	122	83	78	35.3	53.4	24.6	7.3		112
Max	130	88	87	37.8	57.0	28.3	8.2		118
n	9	8	6	8	6	8	7		4
Females: adult									
Mean	127	88	84	36.0	57.3	26.5	8.3		115
SD	1.57	3.51	3.99	0.78	1.88	0.65	0.65		7.68
Min	125	81	78	35.2	55.1	27.5	7.2		108
Max	129	92	81	37.3	58.5	29.6	9.2		125
n	7	7	7	7	3	7	7		4
<i>A. m. mayri</i>									
Males: adult									
Mean	139	92	89.5	37.7	59.8	29.3	8.2	9.5	143
SD	2.99	3.06	2.87	1.86	2.10	0.69	0.64		3.54
Min	134	87	83	33.8	55.4	28.4	7.0		140
Max	145	98	95	40.3	62.4	30.8	9.4		145
n	22	21	20	22	10	21	21		1
immature									
Mean	138	89	87.6	37.6	58.4	28.9	7.9		127
SD	3.37	4.70	5.80	1.00	1.75	1.10	0.60		6.43
Min	131	81	78	35.3	56.7	27.4	6.8		120
Max	143	99	89	38.9	60.7	31.6	8.8		132
n	15	14	13	15	7	15	15		3
Females: adult									
Mean	134	89	86.6	36.4	59.1	30.2	8.6		
SD	3.16	3.83	3.56	0.91	2.11	1.97	0.61		
Min	127	83	80	34.4	54.9	27.3	7.0		
Max	142	98	94	38.1	62.4	38.6	9.8		
n	26	26	25	26	13	28	26		
<i>A. m. kombak</i>									
Males: adult									
Mean	137	87	84	37.4	58.1	28.1	7.4	9.0	125
SD	3.68	3.20	3.69	1.81	1.67	0.90	0.52	0.36	9.27
Min	129	79	73	27.9	55.4	26.5	6.2	8.5	110
Max	144	92	90	40.0	60.7	30.1	8.3	9.5	140
n	37	32	27	38	17	37	35		7
immature									
Mean	135	85	83	37.8	57.9	27.8	7.5	9.0	121
SD	3.66	2.60	2.64	0.97	1.26	0.79	0.60	0.21	9.35
Min	128	80	80	38.2	58.1	28.3	6.7	8.8	110
Max	141	90	88	39.2	59.8	29.6	0.7	9.1	134
n	17	17	17	17	10	17	17		2
Females: adult									
Mean	131	84	81	36.1	57.4	28.8	9.3	9.2	130
SD	3.13	2.92	2.91	1.94	2.31	0.80	0.74	0.48	14.14
Min	127	78	77	30.7	50.0	27.8	7.0	8.8	120
Max	138	98	87	39.8	59.7	30.2	9.8	10.1	140
n	19	18	11	19	15	19	19		2

<i>A. m. nubicola</i>									
Males: adult									
Mean	135	91	90	37.1	58.2	27.8	6.7		128
SD	1.73	3.14	3.85	0.90	0.71	0.95	0.25		5.69
Min	133	89	87	36.2	57.6	26.8	6.4		122
Max	138	95	94	38.0	59.0	28.7	6.9		133
n	3	3	3	3	3	3	3		3
immature									
Mean	134	91	89	36.3	58.7	28.1	7.3		128
SD	1.72	2.51	2.07	1.30	1.55	0.92	0.30		3.95
Min	132	87	85	34.8	56.0	28.8	7.0		125
Max	137	95	92	38.1	60.5	29.5	7.8		135
n	7	7	7	7	7	7	7		7
Females: adult									
Mean	131	89	88	35.5	57.9	28.1	7.6		130
SD	2.85	2.99	2.52	1.21	0.92	0.40	0.26		7.33
Min	128	86	85	33.7	57.0	27.5	7.3		119
Max	137	95	92	36.1	60.5	29.5	7.8		135
n	3	4	3	4	4	4	3		4
<i>A. m. amati</i>									
Males: adult									
Mean	128	82	80.1	35.7		26.2	7.2		
SD	1.41	0.35		1.84					
Min	127	82		34.4					
Max	129	82.5		37.0					
n	2	2	1	2		1	1		
<i>A. m. leucorae</i>									
Males: adult									
Mean	132	82	80	36.8	54.4	27.9	8.0	9.3	
SD	1.87	2.58	3.56	0.95	1.34	1.16	0.57		
Min	130	78	75	35.3	53.4	25.9	7.5		
Max	135	84	84	37.7	55.3	29.7	8.8		
n	5	5	5	5	2	5	5		1
immature									
Mean	131	82	81	36.5		27.8	7.4		
SD	2.00	1.20	2.25	3.48		0.59	0.42		
Min	129	80	79	34.0		27.2	7.1		
Max	133	83	83	38.9		28.3	7.9		
n	3	3	3	2		3	3		
Females: adult									
Mean	129	81	81	37.9		26.6	8.1		
n	1	1	1	1		1	1		
All species									
Males: adult									
Mean	136	88	86	37.2	58.2	28.2	7.8	9.2	123
SD	4.36	4.02	4.16	1.62	1.83	1.07	0.67	0.39	12.33
Min	124	78	73	27.9	53.4	25.9	6.2	8.5	104
Max	145	98	95	40.3	62.4	30.8	9.4	9.6	145
n	102	96	85	101	51	100	98	8	24
immature									
Mean	133	87	85	37.3	57.8	27.8	7.5	9.0	122
SD	4.38	3.90	4.16	1.29	1.56	1.22	0.54	0.21	8.10
Min	122	80	78	34.0	53.4	24.6	6.5	8.8	110
Max	143	99	98	40.6	60.7	31.6	8.8	9.1	139
n	72	70	65	71	46	72	71	2	35
Females: adult									
Mean	132	86	84	36.2	58.1	29.1	8.3	9.2	124
SD	3.64	4.04	3.77	1.27	1.96	1.48	0.65	0.46	8.97
Min	123	78	77	30.7	50.0	26.8	6.6	8.8	108
Max	142	99	94	39.8	62.4	38.6	9.6	10.1	140
n	82	82	89	83	54	83	81	8	17

Amblyornis macgregoriae De Vis, 1890
Macgregor's Bowerbird
(Tables 7 and 22)

♀♀ average 9% wider in bill width than ♂♂, both sexes having all but the same bill length. Mean crest length from posterior base of 47 ♂♂ is 64 (46-75, SD 6.56) and exposed crest length of 96 ♂♂, 82 (52-105, SD 10.26).

Amblyornis macgregoriae macgregoriae
De Vis, 1890

Most similar in size to *kombok* and in proportions, for both sexes, to *nubicola* and *kombok* ♀♀ average 5% wider in bill width than

TABLE 8. Measurements (mm) and weights (g) of *Amblyornis subalaris*.

	Wing length	Tail length	Tail central	Tarsus length	Total head length	Bill length	Bill width	Weight
Males adult								
Mean	125	89	65	34.6	56.4	25.9	7.3	96
SD	2.60	2.87	3.25	1.57	1.44	1.28	0.37	
Min	121	80	77	30.1	54.6	23.5	6.7	
Max	130	94	92	36.7	60.0	28.5	8.0	
n	30	28	27	29	22	23	29	1
subadult								
Mean	123	87	86	34.2	56.5	25.0	7.1	96
SD	1.00	1.15	1.15	1.41	0.42	0.31	0.50	
Min	122	86	85	32.9	56.2	25.1	6.6	
Max	124	88	87	35.7	56.8	25.7	7.6	
n	3	3	3	3	2	3	3	1
immature								
Mean	124	89	86	34.7	55.5	25.9	7.5	109
SD	2.30	2.95	3.39	0.76	1.93	1.00	0.52	8.38
Min	121	84	82	33.5	52.8	24.4	6.6	104
Max	128	93	92	35.9	56.5	27.6	8.5	126
n	11	10	10	11	8	11	11	6
Females adult								
Mean	124	87	85	34.1	56.8	26.5	7.8	109
SD	3.14	2.74	2.36	1.57	1.15	1.18	0.48	9.66
Min	117	81	80	30.7	55.2	24.8	6.7	95
Max	131	92	88	38.4	59.5	29.6	8.5	122
n	22	22	22	22	17	21	21	5

♂♂. Mean crest length from posterior base of 1 ♂ 65 and exposed crest length of 22 ♂♂ 81 (55-92, SD 9.50). Range: W Kukukuku and Herzog Ra to W Owen Stanley Ra, PNG, excluding range of *Am. m. nubicola* to the E (Schodde & McKean, 1973).

Amblyornis macgregoriae germanis
Rothschild, 1910

Both sexes average 7% lighter and fractionally smaller in wing length than *macgregoriae macgregoriae*, but almost identical to it in tail length and similar in tarsus and bill lengths and bill width. Mean crest length from posterior base of 3 ♂♂ 48 (46-50, SD 2.08) and exposed crest length of 10 ♂♂ 68 (56-79, SD 6.51). Range: mountains of Huon Peninsula, PNG.

Amblyornis macgregoriae mayri
Hartert, 1930

The largest subspecies, ♀♀ 5% wider in bill width than ♂♂. Mean crest length from posterior base of 2 ♂♂ 72 (71-73, SD 1.63) and exposed crest length of 22 ♂♂ 90 (79-105, SD 7.79). Range: Weyland Mts. WP to E Star/W Hindenburg Mts, extreme western PNG.

Amblyornis macgregoriae kombok
Schodde & McKean, 1973

Similar in size and proportions to the nominate form. In bill width, ♀♀ average 12% larger than

♂♂. Mean crest length from posterior base of 28 ♂♂ 63 (51-71, SD 4.92) and exposed crest length of 32 ♂♂ 84 (72-93, SD 5.59). Crest rather dense. Throat and upper breast pale-brownish olive; lower breast, abdomen, and under tail-coverts rather bright light buffy brown (Schodde & McKean, 1973). Range: Kubor, Hagen and Bismarek Ra, central PNG, probably W to at least the Strickland R or Hindenberg Ra, and E to Kratke Ra (Schodde & McKean, 1973).

Amblyornis macgregoriae nubicola
Schodde & McKean, 1973

The tail/wing length ratio fractionally longer than average for the species (as in *germanis*). In bill width, ♀♀ average 13% wider than ♂♂. Mean exposed crest length of 3 ♂♂ 83 (75-90, SD 7.75). ♂ crest length from posterior base 59-65 (n=3, SD=3.0) and rather densely leathered, entire under surface uniformly dull coffee-brown. Range: Mt Simpson-Dayman area, E Owen Stanley Ra, probably W to Mt Suckling, PNG (Schodde & McKean, 1973).

Amblyornis macgregoriae amati
Pratt, 1982

2 ♂ specimens indicate this is the smallest subspecies, with wing length closest to *germanis* and tail as in *leeroyae*. Mean crest length from posterior base of 1 ♂ 71 and exposed crest length of 2 ♂♂ 54 (52-57, SD 3.18). Chin, throat and upper breast dark olive brown, only slightly paler than side of head and forehead; breast medium coffee brown. Range: Adelbert Mts, PNG.

Amblyornis macgregoriae leeroyae
Frith & Frith, 1997

A small and particularly short-tailed form, similar to *amati* in size. Tail/wing length averages fractionally shorter than for the species. Of 5 ♂♂, mean crest length from posterior base 64 (62-66, SD 1.64) and exposed crest length 76 (67-83, SD 6.64). Darker and more brown-orange than *kombok*. Range: NNW slopes of Mt Bosavi, PNG.

Amblyornis subalaris Sharpe, 1884
Streaked Bowerbird
(Tables 8 and 22)

Smallest, and relatively shortest winged, *Amblyornis* species. ♀♀ average fractionally smaller than ♂♂. Mean crest length from posterior base of 1 ♂ 50; the exposed crest length of 29 ♂♂ 61 (50-72, SD 5.79), and that of a crested ♀ 30. The species is known to have

TABLE 9. Measurements (mm) and weights (g) of *Amblyornis flavifrons*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width
Males: adult							
Mean	137	85	62	34.2	58.4	30.8	7.9
SD	2.65	1.15	3.46	0.85	1.41	5.78	0.64
Min	135	84	80	33.4	57.4	27.2	7.5
Max	140	86	86	35.1	59.4	37.5	8.6
n	3	3	3	3	2	3	3

hybridised at least once with *Am. macgregoriae*. Range: Mountains of extreme SE of NG, from upper Angabunga R to Mts Suckling, Simpson and Moiba, PNG (Schodde & McKean, 1973).

***Amblyornis flavifrons* Rothschild, 1895**
Golden-fronted Bowerbird
(Tables 9 and 22)

♂ wing length similar to *Am. macgregoriae*. Short-tailed relative to wing length, and long-winged relative to tarsus length, compared with *Am. macgregoriae*. Mean crest length from posterior base of 2 ♂♂ 54 (53-54, SD 0.71) and exposed crest length of 3 ♂♂ 94 (89-97, SD 4.16). No ♀ collected. Range: Foya (or Gaultier) Mts of WP (Diamond, 1982).

***Prionodura newtoniana* De Vis, 1883**
Golden Bowerbird
(Tables 10 and 22)

Immature (♀-plumaged) ♂♂ all-but identical in body measurements to adult ♀♀ but, like adult ♂♂, average slightly smaller in tarsus and bill lengths and notably more so in bill width and depth. The great disparity between ♂ and ♀ tail length, and the relative proportions of these, reflects sexual selection upon ♂♂ for arboreal/flight courtship display traits (Frith & Frith, 2000b,d). Other than this, ♀♀ are fractionally larger, averaging 15% heavier, than ♂♂ but influences of sampling bias upon the latter are unknown. Range: Australian Wet Tropics uplands, from Thornton Ra and Mt Windsor Tableland to Seaview-Paluma Ra, QLD (Nix & Switzer, 1991).

***Sericulus aureus* (Linnaeus, 1758)**
Masked Bowerbird
(Tables 11 and 22)

Both sexes average almost the same wing length. ♀♀ average 5% and 7% larger in tail length and bill width but 7% and 6% smaller in

TABLE 10. Measurements (mm) and weights (g) of *Prionodura newtoniana*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
Males: adult									
Mean	122	110	95	30.3	50.9	23.1	6.0	7.0	73
SD	1.53	3.50	2.24	1.20	0.74	0.54	0.29	0.16	5.13
Min	119	88	85	23.1	49.0	22.0	5.4	6.7	62
Max	126	115	96	32.3	52.4	24.4	7.0	7.4	86
n	74	60	57	57	41	49	55	47	80
subadult									
Mean	119	87	84	29.9	50.7	23.3	6.6	6.9	71
SD	1.26	3.72	1.51	0.89	0.30	1.01	0.46	0.62	2.67
Min	118	79	82	29.0	50.3	21.7	6.2	5.9	68
Max	122	91	86	31.3	51.1	24.3	7.0	7.4	76
n	8	8	7	5	5	5	4	5	7
immature									
Mean	119	88	85.1	30.9	50.0	23.1	6.4	7.16	75
SD	1.76	2.17	2.10	0.67	0.82	0.66	0.40	0.28	3.77
Min	115	84	76	29.2	48.6	21.3	5.4	6.4	69
Max	124	99	90	32.1	51.5	24.2	7.4	8.1	82
n	56	55	52	41	14	42	43	33	42
Females: adult									
Mean	119	88	85	30.6	50.9	23.7	6.8	7.5	84
SD	2.54	1.91	1.94	0.79	2.11	0.70	0.52	0.22	6.36
Min	112	85	80	28.7	47.4	22.3	5.6	7.1	62
Max	124	92	88	32.3	56.4	25.1	7.8	7.8	96
n	30	30	27	28	15	30	29	11	17

bill depth and weight than ♂♂, respectively. With tail/wing length ratio of 60%, this bowerbird has the third shortest proportionate tail. Gilliard's culmen "from base" should be compatible with our bill length, but his 23 for ♂♂ and 24 for ♀♀ are shorter and therefore probably of exposed culmen. Moreover, his ♀ wing length of 137-140 is 2mm shorter than our shortest. Range: Mountains of western and northern NG almost to the Scpik R in the E.

TABLE 11. Measurements (mm) and weights (g) of *Sericulus aureus*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
Males: adult									
Mean	143	84	82	41.4	61.2	30.6	7.5	8.5	178
SD	3.37	3.72	3.55	1.23	1.98	1.61	0.34	0.26	3.54
Min	136	77	76	39.7	57.4	25.9	6.8	7.9	175
Max	151	90	88	44.1	64.8	32.8	8.3	8.8	180
n	22	21	15	18	18	22	22	11	2
subadult									
Mean	147	87	86	42.3	62.9	31.5	7.5	8.6	171
SD	2.86	2.95	3.40	1.44	1.22	1.25	0.52	0.30	7.76
Min	142	81	81	40.3	59.8	29.5	6.6	8.2	165
Max	151	91	92	44.8	64.4	33.1	8.2	8.9	176
n	11	11	9	11	11	11	11	4	2
immature									
Mean	139	90	89	42.0	60.8	32.0	7.5		149
SD	2.63	5.19	8.08	0.73	2.65	1.79	0.68		9.91
Min	135	83	80	41.0	57.3	30.2	6.7		135
Max	141	94	94	42.6	64.2	34.2	8.3		156
n	4	4	3	4	6	4	4		4
Females: adult									
Mean	142	88	87	41.9	61.8	31.5	8.0	7.9	168
SD	2.07	4.81	6.04	1.41	1.00	1.09	0.69	0.14	5.77
Min	139	82	79	40.1	60.4	29.8	8.8	7.8	165
Max	146	97	97	44.7	63.3	33.3	8.9	8.0	175
n	11	10	7	11	10	10	11	2	3

TABLE 12. Measurements (mm) and weights (g) of *Sericulus ardens*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
Males: adult								
Mean	138	65	64	42.2	60.7	29.6	7.4	
SD	4.12	3.02	3.33	2.64	1.28	0.47	0.49	
Min	135	62	60	36.0	58.7	28.8	6.5	
Max	148	72	70	44.6	62.0	30.3	8.1	
n	9	9	8	9	6	8	8	
subadult								
Mean	141	70	67	42.6	59.1	29.0	7.4	
SD	2.99	3.10	3.79	1.72	0.70	0.40	0.58	
Min	138	67	63	40.1	58.4	28.4	6.9	
Max	145	74	70	43.7	59.8	29.3	8.2	
n	4	4	3	4	3	4	4	
Females: adult								
Mean	143	74	73	41.8	59.9	28.9	7.8	
SD	4.95	1.41	2.12	0.07	0.14	0.57	0.07	
Min	139	73	71	41.7	59.8	28.5	7.7	
Max	146	75	74	41.8	60.0	29.3	7.8	
n	2	2	2	2	2	2	2	

Sericulus ardens
(D'Alberty & Salvadori, 1879)
Flame Bowerbird
(Tables 12 and 22)

Sericulus aureus has a tail longer than *Se. ardens* and averages a slightly longer (and pale) bill. This results in strikingly different tail/wing length ratios of 60% and 50%, respectively, the

TABLE 13. Measurements (mm) and weights (g) of *Sericulus bakeri*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
Male: adult								
Mean	138	79	76	41.8	60.1	30.0	8.0	182
SD	1.30	2.35	2.65	0.63	1.02	0.58	0.39	2.12
Min	136	77	73	41.1	58.3	29.0	7.6	180
Max	139	83	80	42.8	60.7	30.4	8.5	183
n	5	5	5	5	5	5	5	2
subadult								
Mean	143	85	83	42.5	60.8	30.6	8.5	178
SD	0.71	2.12	1.41	1.48	0.07	0.21	0.14	
Min	142	83	82	41.4	60.7	30.4	8.4	
Max	143	86	84	43.5	60.8	30.7	8.6	
n	2	2	2	2	2	2	2	1
immature								
Mean	139	83	82	41.8	59.5	29.7	7.7	170
SD	4.95	5.66	7.07	0.49	0.07	0.78	0.49	
Min	135	79	77	41.4	59.4	29.1	7.3	
Max	143	87	87	43.5	60.8	30.7	8.6	
n	2	2	2	2	2	2	2	1
Females: adult								
Mean	139	85	84	40.5	60.6	31.5	8.6	173
SD	3.10	4.13	3.85	1.99	1.47	0.76	0.48	8.38
Min	133	80	80	38.7	58.3	30.6	7.9	164
Max	142	91	91	43.2	62.4	32.9	9.2	184
n	6	6	6	6	5	6	6	5

TABLE 14. Measurements (mm) and weights (g) of *Sericulus chrysocephalus*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Bill depth	Weight
Males: adult									
Mean	130	85	79	34.9	58.5	30.9	5.9	6.9	90
SD	2.56	2.19	2.82	1.26	0.90	0.73	0.30	0.28	12.44
Min	125	82	74	32.5	56.6	29.3	5.5	6.4	76
Max	135	91	86	36.8	60.1	32.3	6.5	7.3	110
n	23	23	22	21	37	21	21	12	5
subadult									
Mean	134	92	85	34.6	56.4	30.6	5.9	7.2	86
SD	2.28	4.65	8.02	1.16	1.95	0.54	0.22	0.26	
Min	131	87	77	33.4	53.6	30.0	5.6	6.9	
Max	137	98	96	36.5	58.0	31.3	6.2	7.4	
n	5	4	4	5	4	4	5	3	1
immature									
Mean	133	99	95	34.6	57.3	30.0	6.1	6.9	90
SD	2.88	2.58	3.10	1.02	1.08	0.87	0.24	0.39	3.90
Min	129	94	91	32.9	55.7	28.8	5.9	6.3	85
Max	140	105	102	36.2	59.0	31.1	6.8	8.0	97
n	14	14	14	14	14	14	14	14	13
Females: adult									
Mean	138	106	102	35.6	57.8	30.4	7.0	7.7	111
SD	3.85	3.36	3.29	1.03	1.13	0.96	0.37	0.29	12.13
Min	131	96	93	34.0	55.7	27.9	6.0	7.1	95
Max	148	111	107	38.2	59.7	32.1	7.5	8.2	134
n	26	26	21	26	26	26	26	23	20

latter having a shorter tail than other bowerbirds (Table 21). Sexual size dimorphism is also quite different in the two species: ♀ *ardens* average 14% and 5% larger in tail length and bill width but fractionally smaller in tarsus and bill lengths than ♂♂. Our bill width figures do not agree well with Lenz's (1999: 53) statement that *ardens* has a "much narrower bill than *aureus*". The bill width figures of Lenz (1999, table 3.8) do not support his statement. They do, however, indicate ♂ *ardens* have a slightly narrower bill than ♂ *aureus* and that *aureus* has a deeper bill than *ardens*. In size differences between the sexes, and in body proportion ratios of the 3 *Sericulus* species in New Guinea, *aureus* differs more from *ardens* than it does from *bakeri*. Range: Patchy in lowlands-foothills from Wataikwa-Mimika, upper Noord-Endrich R of WP to upper Fly R, Strickland-Nomad R and Mt Bosavi, PNG (Mackay, 1984).

Se. a. aureus and *Se. a. ardens* have different ♂ plumages and bill colouration (Cooper & Forshaw, 1977; Beehler et al., 1986). They are all but allopatric, in being isolated by the central ranges, and are restricted to predominantly different altitudes, but do meet and hybridise on the Wataikwa R, south WP as indicated by 1 or 2 ♂♂ specimens (Gilliard, 1969). Thus, *aureus* and *ardens* are considered separate species (Lenz, 1999).

TABLE 15. Measurements (mm) and weights (g) of *Ptilonorhynchus violaceus*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>P. v. violaceus</i>								
Males: adult								
Mean	172	110	103	49.3	66.6	35.4	9.8	238
SD	3.88	5.20	5.45	1.98	1.38	1.70	0.34	19.5
Min	162	103	95	44.3	63.7	31.5	9.0	208
Max	182	125	114	53.0	69.4	40.3	10.4	278
n	66	46	27	47	30	46	46	13
subadult								
Mean	173	115	115	48.3	66.5	35.7	9.7	205
SD	3.77	4.92		2.37	1.51	0.67	0.46	
Min	168	109		45.3	64.8	35.3	9.4	
Max	177	121		50.2	67.7	36.5	10.2	
n	4	4	1	4	3	3	3	1
intermediate-plumaged immature								
Mean	171	119	114	49.3	66.1	34.9	10.1	227
SD	3.98	5.34	4.35	2.38	1.52	1.06	0.29	25.97
Min	161	106	107	43.7	61.7	32.6	9.5	176
Max	178	131	125	53.7	67.7	37.5	10.6	284
n	26	28	18	26	17	28	26	14
female-plumaged immature								
Mean	169	118	111	49.8	65.3	34.3	9.9	225
SD	3.90	4.55	5.50	1.84	1.53	1.08	0.34	8.79
Min	162	107	103	46.7	62.0	32.5	9.2	208
Max	178	126	120	54.2	67.8	35.9	10.4	234
n	21	20	14	21	18	21	21	12
Females: adult								
Mean	165	117	113	46.1	64.1	34.6	10.2	209
SD	4.74	4.67	4.72	2.15	1.50	1.50	0.33	18.80
Min	156	108	102	41.5	60.1	31.0	9.6	170
Max	176	128	123	51.6	67.2	38.2	10.9	250
n	60	59	36	60	43	59	58	30
<i>P. v. minor</i>								
Males: adult								
Mean	153	96	89	47.3	63.9	33.2	9.3	187
SD	2.74	2.80	2.34	1.84	1.20	0.86	0.81	16.70
Min	150	92	87	44.3	62.0	32.0	8.4	173
Max	158	100	93	49.6	65.1	34.4	11.3	205
n	10	10	7	10	7	9	10	4
subadult								
Mean	156	102	97	47.9	64.5	33.4	9.8	206
n	1	1	1	1	1	1	1	1
intermediate-plumaged immature								
Mean	153	101	97	45.9	62.4	32.3	9.8	193
SD	4.85	3.21	3.25	2.35	1.29	0.78	0.37	23.08
Min	144	93	90	41.4	60.5	30.9	9.0	164
Max	165	110	104	48.9	64.2	33.4	10.3	232
n	18	18	17	18	17	18	18	18
female-plumaged immature								
Mean	152	102	98	47.4	62.3	33.3	8.8	197.8
SD	4.73	3.79	2.31	1.18	0.75	0.81	0.15	20
Min	148	99	95	46.7	62.6	32.6	7.9	187
Max	157	106	99	48.8	64.2	34.1	9.5	209
n	3	3	3	3	1	3	3	2
Females: adult								
Mean	150	102	95	45.0	61.5	31.7	9.5	174
SD	4.65	3.32	3.30	1.67	0.21	0.50	0.32	
Min	145	98	91	43.6	61.3	31.3	9.2	
Max	156	106	99	47.0	61.7	32.4	9.9	
n	4	4	4	4	3	4	4	1
All subspecies								
Males: adult								
Mean	169	108	100	48.9	66.1	35.0	9.7	226
SD	7.35	7.46	7.63	2.08	1.70	1.78	0.49	28.65
Min	150	92	87	44.3	62.0	31.5	8.4	173
Max	182	125	114	53.0	69.4	40.3	11.3	278
n	76	56	34	57	37	55	56	17
subadult								
Mean	169	113	106	48.2	66	35.2	9.7	206
SD	8.17	7.30	12.73	2.06	1.59	1.29	0.38	0.71
Min	156	102	97	45.3	64.5	33.4	9.4	205
Max	177	121	115	50.2	67.7	36.5	10.2	206
n	5	5	2	5	4	4	4	2

intermediate-plumaged immature								
Mean	164	111	106	47.9	64.3	33.8	10.0	208
SD	10.22	9.88	9.42	2.88	2.32	1.59	0.35	29.57
Min	144	93	90	41.4	60.5	30.9	9.0	164
Max	178	131	125	53.7	67.7	37.5	10.6	284
n	44	44	35	44	34	44	44	32
female-plumaged immature								
Mean	167	116	109	49.5	65.1	34.2	9.8	221.1
SD	7.07	7.25	7.36	1.93	1.64	1.09	0.55	13.44
Min	148	99	95	46.7	62	32.5	7.9	187
Max	178	126	120	54.2	67.8	35.9	10.4	234
n	24	23	17	24	19	24	24	14
Females: adult								
Mean	164	116	111	46.0	63.9	34.4	10.2	208
SD	6.1	6.0	7.0	2.1	1.6	1.6	0.4	19.5
Min	145	98	91	41.5	60.1	31.0	9.2	170
Max	176	128	123	51.6	67.2	38.2	10.9	250
n	64	63	40	64	46	63	62	31

Sericulus bakeri (Chapin, 1929)
Adelbert Bowerbird
(Tables 13 and 22)

Its tail/wing length ratio is 59%, the second shortest for the family. ♀♀ average 8%, 5% and 8% larger than ♂♂ in tail and bill length and bill width, respectively, but 5% lighter in weight. In most ♀/♂ ratios, as well as tail/wing length for both sexes combined, this (dark-billed) species is more like dark-billed *Se. aureus* than pale billed *Se. ardens*. Gilliard (1969) gave the short bill length "from base" of 23 for ♂♂ and of 24 for ♀♀ (cf. Table 13) but these are probably of exposed culmen. Range: Adelbert Ra, PNG.

Sericulus chrysocephalus (Lewin, 1808)
Regent Bowerbird
(Tables 14 and 22)

Tail/wing length ratio 71%. ♀♀ average 6%, 24%, 19% and 12% larger than ♂♂ in wing and tail lengths and bill width and depth, respectively and average 23% heavier. With increasing age, ♂♂ wings and tails become relatively shorter and their mean central tail feather length gets shorter relative to tail length. As a result, the tail/wing length ratio in ♂♂ is 66% but in ♀♀ is 77%. Lenz (1999:38) gave bill length of 26.0 for ♂♂ and 25.6 for ♀♀. We concur with Hartert (1929) and Schodde & Mason (1999) in considering the doubtful northern *Se. c. rothschildi*, Mathews, 1912 invalid. Range: From N of Sydney to Connors and Clarke Ra, inland of Mackay with a gap at the Fitzroy R valley inland of Rockhampton, Australia.

Ptilonorhynchus violaceus (Vieillot, 1816)
Satin Bowerbird
(Tables 15, 16 and 22)

Tail/wing length ratio 67%, tarsus/wing length 28%, and bill/wing length 21%. ♀♀ average 6%

TABLE 16. Mean measurements of *Ptilonorhynchus v. violaceus*, from N to S of its range in latitudinally bounded subdivisions.

Degress of latitude S Sex/age group	Wing length (n, SD)	Tail length (n, SD)	Tail/wing ratio
26 - 30			
Males: adult	170 (20, 3.07)	107 (20, 4.05)	0.63
immature *	169 (12, 4.40)	114 (12, 4.77)	0.67
Females: adult	164 (9, 4.55)	114 (9, 3.71)	0.7
All birds	169 (41, 4.40)	111 (41, 5.42)	0.66
30 - 32			
Males: adult	172 (22, 3.21)	110 (3, 3.21)	0.64
immature	168 (1)	--	--
Females: adult	166 (4, 7.14)	117 (4, 5.85)	0.7
All birds	171 (27, 4.30)	114 (7, 6.08)	0.67
32 - 34			
Males: adult	174 (6, 6.63)	113 (6, 4.72)	0.65
immature *	172 (16, 3.40)	120 (16, 3.82)	0.7
Females: adult	163 (17, 3.17)	115 (16, 3.66)	0.71
All birds	168 (39, 6.17)	117 (38, 4.78)	0.7
34 - 36			
Males: adult	171 (2, 0.71)	112 (2, 3.54)	0.65
immature	169 (8, 4.34)	117 (8, 4.50)	0.69
Females: adult	166 (2, 7.07)	116 (2, 5.66)	0.7
All birds	169 (12, 4.30)	116 (12, 4.54)	0.69
36 - 39			
Males: adult	174 (10, 4.56)	115 (9, 5.52)	0.66
immature *	171 (13, 3.69)	121 (13, 4.64)	0.71
Females: adult	167 (23, 4.82)	120 (23, 3.97)	0.72
All birds	170 (46, 5.14)	119 (45, 4.85)	0.7

* Samples for 26-30 degrees include two subadults (i.e. immature showing some signs of adult plumage) and for 32-34 and 36-39 degrees one subadult each

and 8% smaller than ♂♂ in tarsus length and weight, but 7% and 5% larger in tail length and bill width. Thus ♂♂ tails become relatively shorter with increasing age. Mean bill length averages 2% shorter in ♀♀ than ♂♂, contrary to comparison of the exposed culmen (Schodde & Mason, 1999). Males in their first to third year have ♀♀-like plumage, but with whiter underparts. In their fourth to sixth year, or prior to attaining subadult characters, their plumage becomes indicative of that of ♂♂ by increasingly solid green breast and throat plumage (Disney, 1970). ♂♂ lacking adult or subadult plumage are '♀-plumaged immature ♂♂'. Birds with any sign of the more solid green breast/throat are 'intermediate-plumaged immature ♂♂'.

Ptilonorhynchus violaceus violaceus
(Vicillot, 1816)

Based on the surgical sexing of 19 birds, and 3 on plumage, caught and measured at Healesville,

Victoria, it was concluded that birds with a tarsus length >57.5 and wing length >161 are ♂♂ and less are ♀♀ (Miller, 1995). Tarsus length measurements of Miller are "tarsus with foot length" of Lowe (1989), thus his are 18% larger than ours. One ♂ of our sample had a wing length of 161, and a tarsus length of 48.9. While our 60 ♀ tarsus lengths are shorter than 58, and thus agree with Miller (1995), 45 ♀♀ had a wing length of 162 or more. Range: coastal Australia in a <250 km band, narrowing to the N, from the Otway Ra W of Melbourne to Dawes Ra, Qld.

Schodde & Mason (1999) described a 'step' in size and tail proportions of the adult (I. Mason pers. comm.) populations in the centre of the range. They wrote that "Within the southern form, there is evidence of incipient divergence at the Hunter River (- Sydney) Barrier, NSW" and go on to observe that "Populations of nominotypical *violaceus* north of the Hunter to northern limits in the Dawes Range (Kroombit plateau), Qld, are relatively small with short tails (wing: ♂♂ c 167-173, ♀♀ c 157-165 mm; tail/wing ratio: ♂♂ c 0.58-0.64, ♀♀ c 0.66-0.70; n = 76). Those S of the Illawarra (Wollongong-Nowra) region are all larger and longer tailed (wing: ♂♂ c 170-178, ♀♀ c 163-170 mm; tail/wing ratio: ♂♂ c 0.63-0.67, ♀♀ c 0.68-0.72; n = 43). In between, from the Hunter to the Illawarra, populations appear to grade from one size morph to the other (n = 65)." Schodde & Mason (1999) claimed that birds N of the Hunter River (or of 32°) are "relatively small with short tails". While our data support this in broadest terms (Table 16) the differences are at best slight, and are less so in adult ♀♀ than in all ♂♂. Schodde & Mason also found birds S of 34° larger and longer tailed, but we find this true of only adult ♀ wing length, as there is little difference in tail/wing length ratio (Table 16).

Mean values for ♂ and ♀ wing length and tail length are compared using Student's two-tailed *t*-test between more pertinent pairs of the five geographical samples (Table 16). Results are as follows: there is no significance in ♂ or in ♀ wing length between the sample pairs of 30-32° and 32-34°, 32-34° and 34-36°, 30-32° and 34-36° S (all being $P > 0.1$). There is also no significance in ♂ and ♀ tail length between these same sample pairs ($P > 0.1$). Wing length between 26-30° and 36-39° S were significant ($P < 0.02$), but ♀ wing length between them was not ($P > 0.1$). Differences in ♂ and in ♀ tail length between these extremes are, however, more significant ($P < 0.001$). The latter differences are

TABLE 17. Measurements (mm) and weights (g) of *Chlamydera maculata*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
Males adult							
Mean	151	109	40.7	59.7	31.5	8.0	139
SD	3.29	4.12	1.56	1.06	1.47	0.46	6.25
Min	145	101	37.6	57.7	28.6	7.0	125
Max	157	117	44.5	61.4	34.9	9.0	150
n	30	30	30	21	29	30	19
subadult							
Mean	150	112	40.4	58.8	31.7	8.1	144
SD	2.6	4.2	1.4	1.0	1.1	0.5	15.5
Min	145	104	37.6	56.9	29.6	7.6	127
Max	154	120	42.5	60.0	34.0	9.1	186
n	22	22	22	11	22	22	12
immature							
Mean	152	117	40.5	58.2	31.3	7.5	117
SD	2.83		1.48		2.55	1.13	
Min	150		39.4		29.5	6.7	
Max	154		41.5		33.1	8.3	
n	2	2	2	1	2	2	1
Females adult							
Mean	146	110	38.9	58.5	31.4	8.2	141
SD	3.44	4.10	1.10	1.47	1.47	0.33	11.71
Min	141	103	36.7	55.4	29.4	7.7	124
Max	156	117	40.8	61.6	35.4	8.9	162
n	30	30	29	26	29	30	13

not surprising, however, given they are between populations at each end of a distribution.

As it is possible that small differences apparent in some sizes for sex/age classes in Table 16 are due to small samples (e.g. for adult ♂♂ of the 32-34° and 34-36°, and adult ♀♀ of the 30-32° and 34-36°) it is worth comparing figures for all birds combined for each zone. These show little difference in wing length for the subspecies, with not even a discernable N-S cline. Our data do not indicate a cline, or step, is in tail/wing length ratio with latitude. Tails are slightly longer in the S than in the N, but even between the N- and S-most zones the difference is minimal (4%) and clinal, with no obvious step (Table 16).

Ptilonorhynchus violaceus minor

A.J. Campbell, 1912

All measurements are about 10% less than in *violaceus violaceus* but body proportions are similar. Plumages are similar but the green of ♀ plumage has a dull bluish-grey cast (Schodde & Mason, 1999). Range: Australian Wet Tropics, from Mt Amos S of Cooktown to Seaview-Paluma Ra, Qld.

Table 15 shows full overlap in wing and tarsus lengths of ♀♀ within the ♂♂ range. Our bill length data (21% of wing length in *violaceus minor* and 20% in *violaceus violaceus*) do not

support the observation that the bill of *violaceus violaceus* is "long and thick" (Schodde & Mason, 1999). This difference from Schodde & Mason (1999) may be due to method of measurement. Their measurement can be misleading, particularly in dimorphic species in which only one sex has modified and/or longer plumage at the base of the upper mandible (Frith & Frith, 1997c: 173). Adult ♂♂ show *minor* to have a bill width 5% narrower than *violaceus violaceus*, and adult ♀♀ *minor* have a bill width 7% narrower than *violaceus violaceus*. For the sexes combined bill width in *minor* is 9.6 and in *violaceus violaceus* 9.9 which, given the difference in their overall sizes, is not striking. The bill of *violaceus violaceus* is not proportionately thicker than that of *minor*. In view of this, we assume Schodde & Mason (1999) meant that the bill of *violaceus violaceus* is long and deep (not thick) and thus "appears stumper in shape" but, like us, they provide no bill depth measurements. Bill width/length is the same in ♂♂ (28%) and ♀♀ (30%) of both subspecies.

Chlamydera maculata (Gould, 1837)

Spotted Bowerbird
(Tables 17 and 22)

Gilliard treated *guttata* as a subspecies of *C. maculata*, but others consider it a distinct species (Frith & Frith, 1997a; Christidis & Boles, 1994; Schodde & Mason, 1999). The tail/wing length ratio is 73%, tarsus/wing length 27%, and bill/wing length 21%. ♀♀ are fractionally smaller than ♂♂, but fractionally larger in bill width and in weight. The species is thus less sexually dimorphic in size than congeners, while being similar in major proportions (Tables 17-21). Immature ♂♂ lack crest feathers, while subadult ♂♂ have some to many. Range: Interior of Qld S of 20° S, except extreme W and SW, and interior of northern and central New South Wales (NSW) (except extreme W border country). Also extreme NW corner of Victoria and just into South Australia (SA), on the Murray R. Once confirmed to have hybridised where it meets *C. melanalis* some 100 km SSE of Charters Towers, Qld (Frith & Frith, 1995b).

Chlamydera guttata Gould, 1862

Western Bowerbird
(Tables 18 and 22)

♀♀ average fractionally smaller than ♂♂ in wing and tarsus lengths, but 5% larger in tail length and bill width, the sexes being the same in total head and bill lengths. Tail/wing length ratio

TABLE 18. Measurements (mm) and weights (g) of *Chlamydera guttata*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>C. g. guttata</i>							
Males: adult							
Mean	149	92	38.9	57.9	30.4	7.4	134
SD	2.47	3.30	1.03	0.95	0.99	0.31	5.17
Min	144	86	36.1	55.7	28.1	6.8	128
Max	157	100	41.6	59.3	32.6	7.9	142
n	34	33	34	31	34	34	8
subadult							
Mean	148	97	39.1	57.8	30.8	7.1	133
SD	1.47	4.49	1.52	0.71	0.34	0.34	4.95
Min	146	90	37.6	56.6	30.2	6.7	129
Max	150	102	41.9	58.6	31.2	7.7	136
n	6	6	6	6	6	6	2
Females: adult							
Mean	147	98	38.1	56.2	30.2	7.7	137
SD	2.36	2.70	1.21	1.24	1.17	0.36	8.20
Min	143	94	35.7	56.1	27.7	6.9	122
Max	152	104	41.0	59.9	31.9	6.4	148
n	21	21	21	17	20	19	9
<i>C. g. carteri</i>							
Males: adult							
mean	135	93	37.3		28.7		7
n	1	1	1		1		1
Females: adult							
Mean	137	91	36.5	57.1	30.5	7.7	
SD	2.88	3.33	0.57		0.81	0.38	
Min	135	87	35.5		29.7	7.1	
Max	141	95	37.2		32.0	8.2	
n	6	6	6	1	6	6	
All subspecies							
Males: adult							
Mean	148	92	38.9	57.9	30.4	7.3	134
SD	3.36	3.26	1.05	0.95	1.02	0.31	5.17
Min	135	86	36.1	55.7	28.1	6.8	128
Max	157	100	41.6	59.3	32.6	7.9	142
n	35	34	35	31	35	35	8
subadult							
Mean	148	97	39.1	57.8	30.8	7.1	133
SD	1.47	4.49	1.52	0.71	0.34	0.34	4.95
Min	146	90	37.6	56.6	30.2	6.7	129
Max	150	102	41.9	58.6	31.2	7.7	136
n	6	6	6	6	6	6	2
Females: adult							
Mean	145	97	37.8	58.1	30.3	7.7	137
SD	4.90	4.30	1.31	1.23	1.09	0.36	8.20
Min	135	87	35.5	56.1	27.7	6.9	122
Max	152	104	41.0	59.9	32.0	8.4	148
n	27	27	27	18	26	25	9

65%, tarsus/wing length 26%, and bill/wing length 21%, the first of these confirming the short tail (8% shorter than *C. maculata*).

This Australian taxon was treated as a separate species until Mathews (1912) considered it a subspecies of *C. maculata*. We agree with Schodde (1982) that *guttata* is a separate species. For diagnosis see Schodde & Mason (1999).

TABLE 19. Measurements (mm) and weights (g) of *Chlamydera nuchalis*.

	Wing length	Tail length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>C. n. nuchalis</i>							
Males: adult							
Mean	182	144	49.1	69.0	38.7	9.0	216
SD	5.73	6.83	1.90	1.54	1.30	0.55	27.94
Min	171	133	45.6	65.5	36.0	7.9	180
Max	193	157	54.6	71.8	40.8	10.6	265
n	35	35	35	26	34	35	9
subadult							
Mean	180	144	48.4	69.5	39.1	9.0	222
SD	4.80	5.93	1.38	1.02	1.28	0.43	12.36
Min	170	135	44.3	68.1	36.8	7.9	201
Max	189	157	49.8	72.0	41.0	9.5	240
n	17	17	17	12	16	17	9
immature							
Mean	179	151	49.2	68.9	39.0	8.5	213
SD	7.83	7.51	2.18	2.12	1.53	0.49	17.30
Min	163	138	44.4	65.2	36.5	7.4	195
Max	196	165	54.0	73.2	41.6	9.3	242
n	31	31	31	18	28	30	10
Females: adult							
Mean	173	143	45.7	66.9	37.6	8.8	188
SD	6.89	7.49	1.80	1.48	1.65	0.47	14.15
Min	158	127	42.3	64.2	32.2	7.6	164
Max	191	160	50.5	69.7	41.5	9.8	215
n	51	50	51	35	50	50	17
<i>C. n. orientalis</i>							
Males: adult							
Mean	175	131	46.9	68.5	38.4	8.9	210
SD	3.59	4.50	2.00	1.48	1.69	0.49	13.53
Min	167	122	43.1	65.4	34.5	8.2	187
Max	182	139	52.6	71.6	41.4	10.1	236
n	26	26	26	15	26	26	10
subadult							
Mean	177	134	47.4	67.6	37.8	8.8	240
SD	5.21	5.08	1.53	1.56	1.78	0.55	56.46
Min	168	124	44.6	65.9	35.2	8.1	187
Max	186	145	50.2	70.3	41.7	9.7	317
n	15	15	15	6	15	14	5
immature							
Mean	169	134	46.1	66.8	37.3	8.6	200
SD	6.98	7.38	1.92	1.22	1.54	0.51	10.67
Min	156	121	41.5	63.9	35.0	8.0	188
Max	186	149	50.7	68.1	39.9	9.8	213
n	32	32	32	11	32	32	5
Females: adult							
Mean	167	131	43.8	65.6	36.9	8.7	168
SD	5.55	5.26	1.73	1.74	1.47	0.53	15.58
Min	155	122	40.7	62.9	32.6	7.7	153
Max	177	142	46.9	67.6	38.6	9.9	205
n	33	33	33	14	32	32	13
All subspecies							
Males: adult							
Mean	179	138	48.2	68.8	38.6	9.0	212
SD	5.08	5.91	2.24	1.52	1.47	0.53	21.17
Min	167	122	43.1	65.4	34.5	7.9	180
Max	193	157	54.6	71.8	41.4	10.6	265
n	61	61	61	41	60	61	19
subadult							
Mean	179	139	47.9	68.8	38.5	8.9	228
SD	5.10	7.26	1.51	1.50	1.65	0.49	34.04
Min	168	124	44.3	65.9	35.2	7.9	187
Max	189	157	50.2	72.0	41.7	9.7	317
n	32	32	32	18	31	31	14
immature							
Mean	174	142	47.6	68.1	38.1	8.6	209
SD	8.81	11.09	2.56	2.06	1.75	0.50	16.36
Min	158	121	41.5	63.9	35.0	7.4	188
Max	196	165	54.0	73.2	41.6	9.8	242
n	63	63	63	29	60	62	15
Females: adult							
Mean	170	138	44.9	66.6	37.4	8.7	187
SD	6.86	8.71	2.01	1.65	1.57	0.49	14.56
Min	155	122	40.7	62.9	32.2	7.6	153
Max	191	160	50.5	69.7	41.5	9.9	215
n	84	83	84	49	82	82	30

TABLE 20. Measurements (mm) and weights (g) of *Chlamydera cerviniventris*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
Australia								
Males: adult								
Mean	140	112		41.4	61.4	30.6	7.6	175.
SD	3.30	3.36		0.35	1.46	1.08	0.44	4.73
Min	141	105		39.4	58.7	28.4	6.6	170
Max	154	116		42.9	62.9	32.1	6.7	182
n	24	24		24	5	22	25	7
Females: adult								
Mean	144	111	104	39.1	50.4	30.5	8.1	157
SD	3.98	3.71		1.42	1.02	1.03	0.31	9.78
Min	138	104		36.8	59.1	28.4	7.6	144
Max	150	118		41.5	61.8	32.7	8.5	167
n	19	17	1	16	6	17	19	5
New Guinea								
Males: adult								
Mean	149	111	105	41.0	59.6	30.8	6.2	159
SD	4.15	2.69	2.07	1.45	5.61	1.15	0.4	10.66
Min	141	107	104	38.4	39.6	28.1	7.4	145
Max	157	117	109	43.3	64.2	33.7	9.1	180
n	37	35	6	35	32	36	35	37
Females: adult								
Mean	146	111	105	39.3	50.5	30.9	8.3	149
SD	4.02	2.97	2.49	1.42	1.44	1.14	0.89	13.65
Min	139	105	104	34.7	57.2	29.0	7.0	117
Max	156	119	110	42.2	65.5	34.9	10.5	170
n	32	32	5	33	29	33	33	16
All birds								
Males: adult								
Mean	148	112	106	41.2	60.1	30.7	8.0	162
SD	3.81	2.99	2.07	1.25	5.20	1.13	0.50	11.46
Min	141	105	104	38.4	39.6	28.1	8.4	145
Max	157	118	109	43.3	64.2	33.7	9.1	182
n	51	60	6	59	38	58	58	44
Females: adult								
Mean	145	111	105	39.3	60.5	30.8	8.2	151
SD	4.10	3.22	2.40	1.41	1.37	1.10	0.58	13.19
Min	138	104	104	34.7	57.2	29.4	7.0	117
Max	156	119	110	42.2	65.5	34.9	10.5	170
n	50	49	6	51	35	50	51	21

Chlamydera guttata guttata Gould, 1862

The larger subspecies, blacker dorsally and with a longer and broader nuchal crest. ♂♂ have crests and ♀♀ vary from no crest to a complete one. Range: Western Australia (WA), from the base of North West Cape through the Pilbara and into the central interior. Thence E in a narrowing band, across the Northern Territory (NT) border into the S of NT to c. 200-300 km N and E of Alice Springs, and extending 100 km S of the NT/SA border and E to due S of Alice Springs.

Chlamydera guttata carteri Mathews, 1920

Averages 8% smaller in wing length and 5% in tarsus length than the nearest populations of *guttata guttata* (Hammersley R, Onslow & Sherlock R areas) but only fractionally so in tail and bill lengths. Thus *carteri* has a long (and

broad) bill, in addition to being richer and more russet coloured than *guttata guttata* (Frith & Frith, 1997a). Five of six ♀♀ examined have a full ♂-like crest. Range: Restricted to North West Cape, WA.

Chlamydera nuchalis (Jardine & Selby, 1830) Great Bowerbird (Tables 19 and 22)

Adults have tail/wing length ratio 79%, tarsus/wing length 27%, bill/wing length 22%. ♀♀ average 5%, 7% and 12% smaller than ♂♂ in wing and tarsus lengths and weight, respectively. All adult ♂♂ have a full crest, and the 17 subadult ♂♂ have between 10 crest feathers to three-quarters of a full ♂-like crest. Of 84 ♀♀, none have a full ♂-like crest while 4 have only 4-10 crest feathers, 2 a quarter-developed crest, 3 a third-, 1 a half-, and 1 a three-quarter developed crest (Frith & Frith, 1999).

Chlamydera nuchalis nuchalis (Jardine & Selby, 1830)

Chlamydera nuchalis oweni Mathews, 1912.

The larger subspecies, ♀♀ average 5% smaller than ♂♂ in wing length, 7% smaller in tarsus length and 14% lighter. Mean ratios for sexes combined are: tail/wing length 81%, tarsus/wing 27%, bill/wing 22%. We agree with Mayr & Jennings (1952), Gilliard (1969) and Hall (1974) that this subspecies has paler and less contrasting, more uniform and greyish, upperparts and underparts usually darker than *orientalis*. Immatures exhibit slight and faint ventral (mostly flank) barring (stronger in some more W individuals), but adults less so or not at all. Adults typically lack silky silvery-white feather tipping, or spotting, throughout the crown (and when present only about the pink nuchal crest feathers). Range: Kimberley, NT, extreme NW Qld, islands off N coast, to no further S than 20° S.

Chlamydera nuchalis orientalis Gould, 1879

Chlamydera nuchalis yorki Mayr & Jennings, 1952

The smaller subspecies, averaging 9% smaller in tail length, and fractionally so in tarsus and bill lengths and bill width than *nuchalis nuchalis*. Similar to *nuchalis nuchalis* in ♀ size as proportion of. Mean combined sexes tarsus/wing length and bill/wing length ratios the same as *nuchalis nuchalis*, but tail/wing 77% (Frith & Frith, 1999). Dorsal colouration and markings (Mayr & Jennings, 1952) are darker and more variegated or contrasting in pattern. Ventral

TABLE 21. Measurements (mm) and weights (g) of *Chlamydera lauterbachii*.

	Wing length	Tail length	Tail central length	Tarsus length	Total head length	Bill length	Bill width	Weight
<i>C. l. lauterbachii</i>								
Males: adult								
Mean	133	104		39.7	57.0	27.5	6.9	135
SD	1.41	2.83		0.21		1.70	0	
Min	132	102		39.5		26.3	6.9	
Max	134	106		39.8		28.7	6.9	
n	2	2		2	1	2	2	1
<i>C. l. uniformis</i>								
Males: adult								
Mean	134	106	99	38.6	56.3	28.1	6.9	130
SD	2.67	3.39		1.59	1.51	0.87	0.29	3.89
Min	130	100		34.8	52.6	26.3	6.4	128
Max	139	112		41.4	57.8	29.6	7.5	133
n	21	20	1	22	10	22	21	2
Females: adult								
Mean	131	106	102	37.5	56.6	28.2	7.2	115
SD	2.82	4.25	1.73	1.47	1.29	0.69	0.34	4.16
Min	125	99	100	35.3	53.9	26.6	6.2	112
Max	137	116	103	41.1	58.2	29.5	7.8	120
n	26	26	3	26	12	26	26	3
All subspecies								
Males: adult								
Mean	134	106	99	38.7	56.3	28.0	6.9	132
SD	2.58	3.34		1.55	1.45	0.92	0.27	3.88
Min	130	100		34.8	52.6	26.3	6.4	128
Max	139	112		41.4	57.8	29.6	7.5	135
n	23	22	1	24	11	24	23	3
Females: adult								
Mean	131	106	102	37.5	56.6	28.2	7.2	115
SD	2.82	4.25	1.73	1.47	1.29	0.69	0.34	4.16
Min	125	99	100	35.3	53.9	26.6	6.2	112
Max	137	116	103	41.1	58.2	29.5	7.8	120
n	26	26	3	26	12	26	26	3

plumage, particularly flanks, usually strongly barred. Birds in the NE (formerly *yorki*) average slightly smaller and paler, more so ventrally and particularly on the throat, than those to the S (Frith & Frith, 1999). Range: Qld N of 20° S, a little further S in the E. Absent on Cardwell-Tully coast and E watershed of the Wet Tropics ranges. Locally sympatric with *C. cerviniventris* on NE Cape York Peninsula, but hybrids unknown.

Gilliard (1969) followed Mayr & Jennings (1952) in accepting 4 subspecies. Now *oweni* is considered a synonym of *nuchalis* and *yorki* is synonymous with *orientalis* (Frith & Frith, 1999; Schodde & Mason, 1999). Colouration and pattern of the crown are important discriminators in *Ailuroedus*, *Amblyornis* and *Chlamydera* (Gilliard, 1969; Frith & Frith, 1995b, 1997a,b, 1998). The marked difference in crown and dorsal plumage colouration and pattern separate *nuchalis*, in WA and the NT east to the Gulf of Carpentaria in W Qld from *orientalis* in the E and

NE of Australia (Storr, 1967, 1973, 1977, 1980, 1984; Ford, 1974, 1987; Schodde, 1986). See *C. maculata* (above) for details of hybridisation.

***Chlamydera cerviniventris* Gould, 1850**
Fawn-breasted Bowerbird
(Tables 20 and 22)

There is negligible difference between NG and Qld populations (Table 20). Tail/wing length ratio is 76%, tarsus/wing length 27%, and bill/wing length 21%. ♀♀ average 5% smaller in tarsus length and are 7% lighter than ♂♂. Range: PNG coast to 500 m asl, to Humboldt Bay in N and Marauke in the S of WP. Jimi Valley, PNG at 1700 m (Frith, 1987). Locally sympatric with *Lauterbach's* but hybrids unknown. Isolated populations in Ransiki and Kebor Valleys of E Vogelkop; along eastern coastal zone of Cape York Peninsula to Coen, Qld where locally sympatric with Great Bowerbird but hybrids unknown.

***Chlamydera lauterbachii* Reichenow, 1897**
Lauterbach's Bowerbird
(Tables 21 and 22)

Tail/wing ratio of 80%, tarsus/wing 29%, and bill/wing 21%; ♀♀ 13% lighter than ♂♂.

Chlamydera lauterbachii lauterbachii
Reichenow, 1897

Known from two specimens, with coppery coloured crown and cheek feathering having a *Sericulus*-like metallic rose-golden sheen to it. Range: Aiome area of upper Ramu R, PNG, possibly also near Bogadjim, Finisterre Mts, PNG (Gilliard & LeCroy, 1968).

Chlamydera lauterbachii uniformis
Rothschild, 1931

No differences between this and *lauterbachii lauterbachii* in average sizes or body proportions. Crown yellowish olive-green (50). Range: NG lowlands to 1800m asl, from Geelvink Bay, WP to Okapa-Aiyura area of E Highlands, PNG. Patchy in Snow and Star Mts to upper Ramu R. Sympatric with *C. cerviniventris* SE of Hupai, Ramu Valley, and in Aiyura Valley (Bailey, 1992; Doyle et al., 1981), but hybrids unknown.

CONCLUSIONS

It has been stated that sexual size dimorphism, expressed by the ♂/♀ wing length, is no greater in polygynous bowerbirds than in monogamous *Ailuroedus* species (Payne, 1984). Polygynous *Sc. dentirostris* is, however, less sexually

TABLE 22. Mean size and some mean body proportions of adult ♀ vs ♂ bowerbirds, expressed as % ♀ are smaller than ♂ or as a % of mean size the former trait is of the latter. Values of less than 5% are not indicated. Tables 1-21 give sample sizes. MWL = mean wing length; MTL = mean tail length; MLL = mean tarsus length; MBL = mean bill length; MBW = mean bill width; MBD = mean bill depth; MW = mean weight.

Species	FEMALE/MALE							MTL/MWL (male, female)	MLL/MWL	MBL/MWL
	MWL	MTL	MLL	MBL	MBW	MBD	MW			
<i>Al. buccoides</i>	-	5*	5	5	6	7	9	66 (67.66)	28	22
<i>Al. crassirostris</i>	-	-	-	-	-	-	10	74 (74.74)	28	20
<i>Al. melanotis</i>	-	-	-	-	5	5	8	73 (73.73)	29	23
<i>Sc. dentiostriis</i>	-	-	-	-	-	-	7+	70 (70.69)	21	21
<i>Ar. papuensis</i>	8	22	9	-	-	-	-	96 (103.88)	26	21
<i>Am. inornatus</i>	-	-	-	-	-	-	5	70 (71.70)	27	23
<i>Am. macgregoriae</i>	-	-	-	-	9	-	-	65 (65.65)	27	21
<i>Am. subalans</i>	-	-	-	-	-	-	-	70 (70.70)	28	21
<i>Am. flavifrons</i>	-	-	-	-	-	-	-	62 (62.-)	25	22
<i>Pr. newtoniana</i>	-	20	-	-	13+	7+	15+	82 (90.74)	25	19
<i>Se. aureus</i>	-	5+	-	-	7+	7	6	60 (59.62)	29	22
<i>Se. ardens</i>	-	14+	-	-	5+	-	-	50 (47.52)	30	21
<i>Se. bakeri</i>	-	8+	-	7+	8+	-	5	59 (57.61)	30	22
<i>Se. chrysocephalus</i>	6+	24+	-	-	19+	12+	23+	71 (66.77)	26	23
<i>Pt. violaceus</i>	-	7+	6	-	5+	-	8	67 (64.71)	28	21
<i>C. maculata</i>	-	-	-	-	-	-	-	73 (72.74)	27	21
<i>C. guttata</i>	-	5+	-	-	5+	-	-	65 (62.67)	26	21
<i>C. nuchalis</i>	5	-	7	-	-	-	12	79 (77.81)	27	22
<i>C. cerviniventris</i>	-	-	5	-	-	-	6	76 (76.77)	27	21
<i>C. lauterbachii</i>	-	-	-	-	-	-	13	80 (79.81)	29	21
Mean of mean ratios								71	27	21

dimorphic in size than *Ailuroedus* (Tables 1-4, 22). Our wing length data agree with Payne (1984) in demonstrating *Ar. papuensis* to be the most sexually dimorphic bowerbird in this trait. They also agree with Lenz (1999) in showing *Se. chrysocephalus* to be the second most sexually dimorphic (but reversed, in that ♀♀ are larger than ♂♂) and not the least dimorphic bowerbird (pace Payne, 1984). In all polygynous bowerbird genera except *Sericulus* ♀♀ are typically shorter in wing and tarsus lengths than ♂♂. In all bill dimensions ♀♀ *Ailuroedus* average slightly smaller than ♂♂, whereas in the majority of polygynous species ♀♀ have bills the same size or larger than ♂♂. We consider the morphology and geographical isolation of *Al. crassirostris* supportive of its distinct status from *Al. melanotis*, this being in harmony with the separation of *Se. ardens* and *C. guttata*.

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